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RHODOPETALINAE, A NEW SUBFAMILY OF ACMAEIDAE FROM THE BOREAL PACIFIC: ANATOMY AND SYSTEMATICS

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ABSTRACT

Doubt concerning the familial assignment of the patellacean limpet *Rhodopetala rosea* (Dall, 1872) has existed since the species was described. The shell morphology and structure are patellid features, while the radular teeth configuration is distinctly acmaeid. The anatomy of *R. rosea* is basically acmaeid, but there are several significant differences and patellid features. The gill is located in the nuchal cavity and is rudimentary. Its structure is analogous to the individual lappets that form the secondary gill found in the mantle groove of patellid limpets and some acmaeids. The gill lacks filaments, a septum, distinct ciliated bands, and skeletal support and arises from the mantle skirt rather than the posterior wall of the nuchal cavity. Correspondingly, the vessels of the auricle are modified to receive blood from the haemocoelic spaces in the nuchal cavity roof. In addition, the circumpallial vessel connects with the haemocoelic spaces rather than directly with the auricle. The anterior portions of the right and left excretory organs extend above the nuchal cavity within the mantle skirt. Structures of the digestive system—looping of the alimentary tract and radular sac, radular dentition—are acmaeid features, while the position of the gonad is like that seen in patellid limpets. Modifications of the respiratory and circulatory systems may be adaptations associated with the brooding behavior of the species. The unique shell structure of this acmaeid limpet and the anatomical characters warrant a new subfamiliar category within the family Acmaeidae.

Rhodopetalinae subfam. nov. is distinguished from other acmaeid subfamilies by a helcioniform rather than conical shell, an interior central area with a silvery metallic lustre rather than a porcelaneous central area, and the presence of a rudimentary gill without typical ctenidial structures. The combination of the patellid shell structure and acmaeid-like anatomy suggest that the Rhodopetalinae is an ancestral intermediate group between the acmaeid and cellanid limpets.

INTRODUCTION

The superfamily Patellacea Rafinesque, 1815 includes three Recent families: Acmaeidae Forbes, 1850; Lepetidae Dall, 1869, and Patellidae Rafinesque, 1815 (Knight et al., 1960). Members of these subfamilies have a docoglossate radula, subcentral to anterior shell apex, and a horseshoe-shaped myostracum (muscle scar). Families are distinguished by anatomical criteria. Acmaeid limpets are the only patellaceans with a ctenidium, in addition, some species also have a secondary gill (branchial cordon). In the Lepetidae gills are completely lacking, respiratory exchange taking place in the lining of the mantle groove (Powell, 1973). In members of the Patellidae only a secondary gill is present. Radular teeth configurations can also be used to distinguish families, however, dentition is more useful for distinguishing genera within families.

MacClintock (1967) introduced a new character into patellacean systematics: shell structure. MacClintock found 17 different types of crystal structure and layering in Recent and fossil patellacean shells, 10 in the Patellidae, 8 in the Acmaeidae, and 1 in the Lepetidae. Thus, the gill, radular, and shell structure characters of each of the 3 families, taken in aggregate, clearly delineate and define them, despite some shared characters such as secondary gills and shell structure (Table 1).

While preparing a revision of the Acmaeidae I took under study the familial assignment of the small boreal patellacean, *Rhodopetala rosea* (Dall, 1872). Doubt concerning the familial assignment of this species has existed since the species was described. In the original description *R. rosea* was questionably as-

TABLE 1. Characters of Recent Patellacean Limpets

Taxon	Shell structure group no.[1]	Radula (M-L-R-L-M)[2]	Gill
Family Patellidae			
Genus *Patella*	6, 8	3-3-0-3-3	complete secondary gill
	6, 8, 9, 10	3-3-1-3-3	complete secondary gill
Genus *Helcion*	6, 7	3-3-0-3-3	incomplete secondary gill
	6	3-3-1-3-3	incomplete secondary gill
Genus *Cellana*	12, 13, 14	3-2-0-2-3	incomplete secondary gill
Genus *Nacella*	11	3-2-0-2-3	complete secondary gill
Family Acmaeidae			
Genus *Acmaea*	15	0-3-0-3-0	ctenidium
Genus *Pectinodonta*	15	0-3-0-3-0[3]	ctenidium
Genus *Tectura*	1	0-3-0-3-0[4]	ctenidium
Genus *Rhodopetala*	12	0-3-0-3-0	rudimentary gill
Genus *Notoacmea*	1, 4, 5	0-3-0-3-0[5]	ctenidium
Genus *Problacmaea*	2	0-3-0-3-0	ctenidium
Genus *Collisella*	1, 16	1-3-0-3-1	ctenidium
Genus *Lottia*	1	1-3-0-3-1	ctenidium & secondary gill
Genus *Scurria*	3	1-3-0-3-1	ctenidium & secondary gill
Genus *Patelloida*	2	2-3-0-3-2	ctenidium
Family Lepetidae			
Genus *Lepeta*	15	2-2-0-2-2	absent
Genus *Cryptobranchia*	15	2-2-0-2-2	absent

[1]After MacClintock (1967).
[2]M = # of marginal teeth, L = # of lateral teeth, R = # of rachidian teeth.
[3]Multicuspid lateral teeth.
[4]Basal plates simple.
[5]Basal plates complex.
MacClintock's (1967) shell structure group no. 17 restricted to Eocene patellaceans.

signed to the genus *Nacella* Schumacher, 1817 in the family Patellidae. This familial assignment was followed by Pilsbry (1891), who placed the species in the genus *Patella,* subgenus *Helcion* Montfort, 1890 because of the submarginal apex. Dall (1921) changed his original familial assignment and established *Rhodopetala,* by monotypy and without explanation, as a section of the Acmaeidae. Oldroyd (1927), Keen (1937), and Burch (1946) all followed Dall and considered *R. rosea* to be an acmaeid.

Keen (1960) transferred *Rhodopetala* back to the family Patellidae, placing it as a subgenus of *Helcion.* McLean (1966) also considered *R. rosea* to be a patellid, and treated it as a subgenus of *Ansates* Sowerby, 1839, regarded by Keen (1960) and McLean (1966) as the prior name for *Patina* Gray, 1847. MacClintock (1967), after studying the shell structure, assigned *Rhodopetala* as a subgenus of the patellid genus *Cellana* H. Adams, 1869.

All of these workers utilized characters found in the shell because whole animals were unknown. Golikov & Kussakin (1972) published on the first known whole specimens of *R. rosea,* indicating its ovoviviparity and the distinct acmaeid configuration of the radular teeth. They placed it in the family Tecturidae Gray, 1847 [= Acmaeidae]. Powell (1973), in a monograph of the Patellidae and Christiaens (1976), in a revision of the Acmaeidae, have also considered *R. rosea* to be an acmaeid. However, there has remained the paradox of the shell structure being patellid (MacClintock, 1967) and the radula being acmaeid (Golikov & Kussakin, 1972). The absence of specialized respiratory structures (Golikov, personal communication, 1978), a lepetid character, further obscures the familial position of these limpets.

In the present paper aspects of the anatomy of *R. rosea* are described and illustrated for the first time. The findings of this study have caused me to reconsider my earlier familial assignment (Lindberg, 1977) and I now consider *R. rosea* to belong to the family Acmaeidae. Because much of the anatomy of *R. rosea* differs so little from previously stud-

ied acmaeids, only specific characters, significant anatomical differences, and diagnostic familial characters are presented and discussed. However, several of the anatomical differences are significant enough to warrant subfamilial rank and I therefore propose a new subfamily within the Acmaeidae.

MATERIALS AND METHODS

Specimens of *R. rosea* were collected by C. E. O'Clair from intertidal areas on Amchitka Island, Aleutian Islands, Alaska in 1971, 1972, and 1974 (Table 2). The limpets were fixed in 10% formalin and then placed in 70% isopropyl alcohol. A single specimen was dehydrated, cleared, and embedded in paraffin. Serial, transverse sections were cut on a microtome at 10 μm and stained with haemotoxylin and eosin.

The organ systems were reconstructed from the sections by mapping the dimensions and positions of structures at intervals of 50 μm or less. Four additional specimens were dissected to corroborate the reconstructions. The tissue sections and radula preparations are deposited in the Natural History Museum of Los Angeles County.

Unless otherwise stated, organs and structures are illustrated as viewed in the dorsal aspect with the anterior towards the top of the page.

TABLE 2. Material examind.

Specimen no.	Size (mm)	Sex	Depository	Remarks
1	3.6	♂	1	sectioned
2	4.8	♀	1	
3	5.5	ind.	1	dissected
4	7.6	♀	1	dissected
5	8.5	♂	1	dissected
6	4.7	♀	2	
7	4.8	♀	2	
8	5.4	ind.	2	
9	5.8	♂	2	
10	7.3	♂	2	
11	8.6	♀	2	dissected

ind. = indeterminate; 1 = Natural History Museum of Los Angeles County #71-252; 2 = National Museum of Natural Science, Ottawa #1976-30.

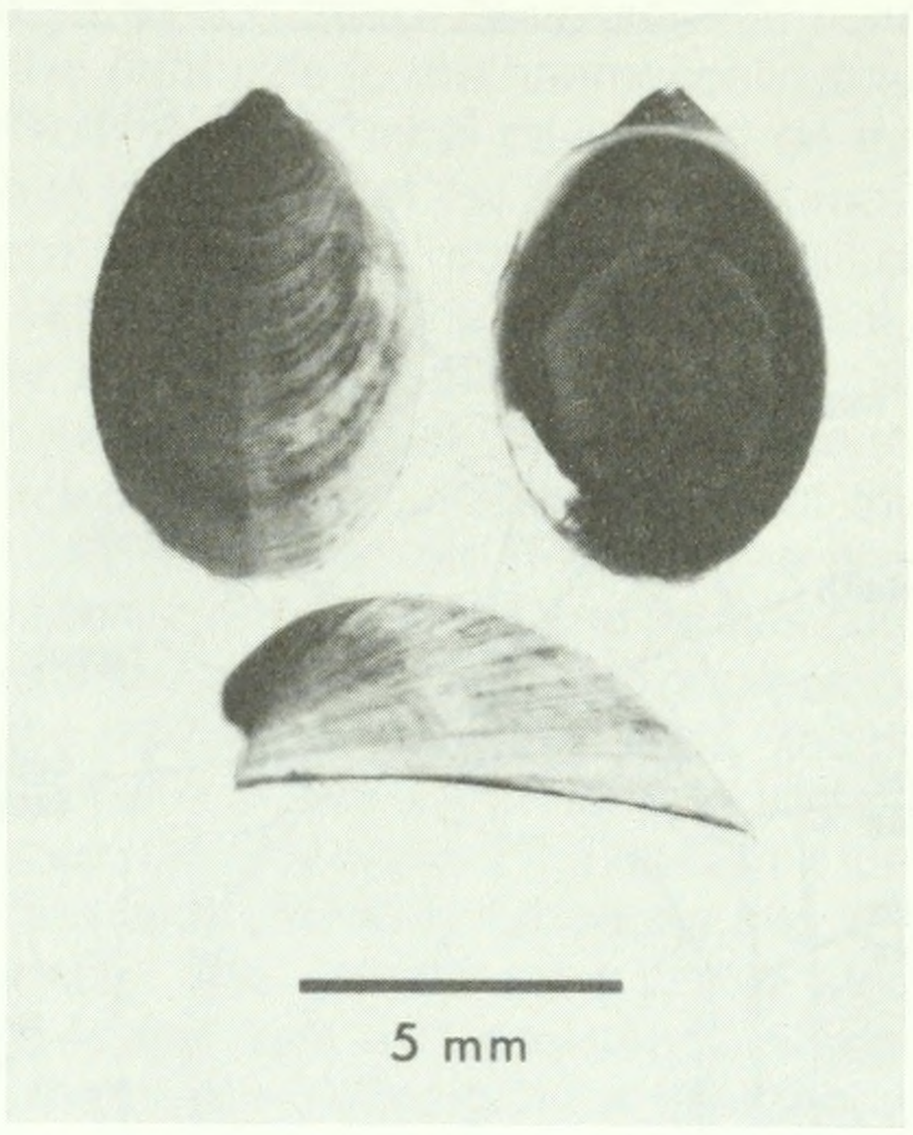

FIG. 1. *Rhodopetala rosea* (Dall, 1872) (Natural History Museum of Los Angeles County #71-252).

ANATOMY

Shell

The shell (Fig. 1) is small (less than 10 mm long), and of medium height; the apex overhangs the anterior margin. The anterior slope is concave and the posterior and lateral slopes convex. The aperture is ovoid and the sides subparallel. Exterior sculpture consists of concentric growth lines and obsolete radial ribs. Shell color ranges from pink to red, but the apex typically is eroded to white. The interior margin of the shell also ranges from pink to red. The intermediate area is red, but changes to white in wet preserved specimens. The myostracum is horseshoe-shaped and opens broadly anteriorly. A fine pallial line connects the anterior portions of the myostracum. The central area, in both dry and wet preserved specimens, is silvery white.

Rhodopetala rosea belongs to MacClintock's (1967) shell structure group no. 12 (Fig. 2). The exterior of the shell and interior margin consist of a complex prismatic layer. Two layers are present in the intermediate area. Nearest to the interior margin the shell structure is foliated. This is followed by a radial crossed-lamellar layer that extends to the myostracum. Interior of the myostracum the central area is composed of a complex crossed-lamellar layer. Altogether there are 5 layers including the myostracum.

External anatomy

Removed from the shell and viewed in the ventral aspect (Fig. 3), the foot is small and subcircular, covering approximately 60% of

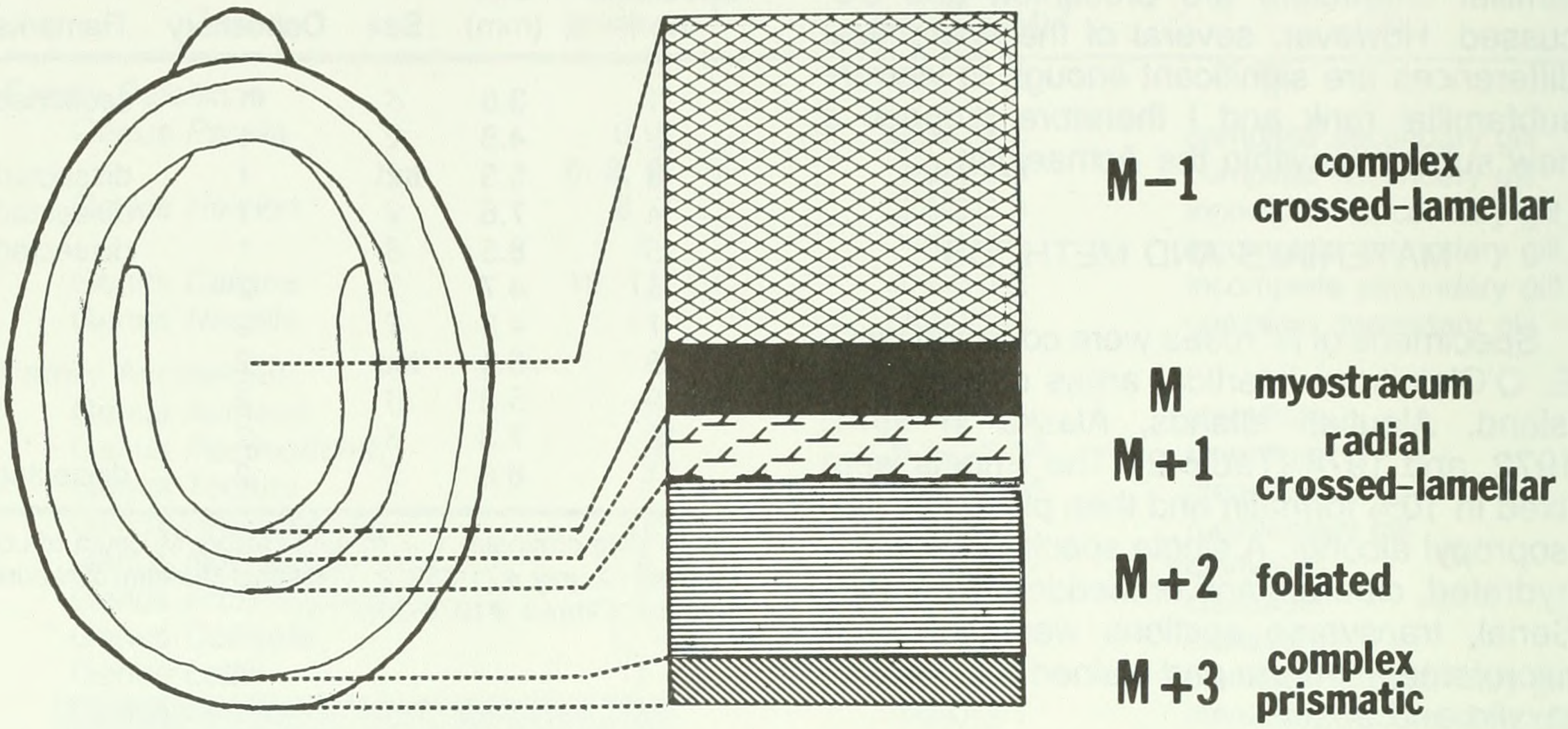

FIG. 2. Shell structure of *Rhodopetala rosea*.

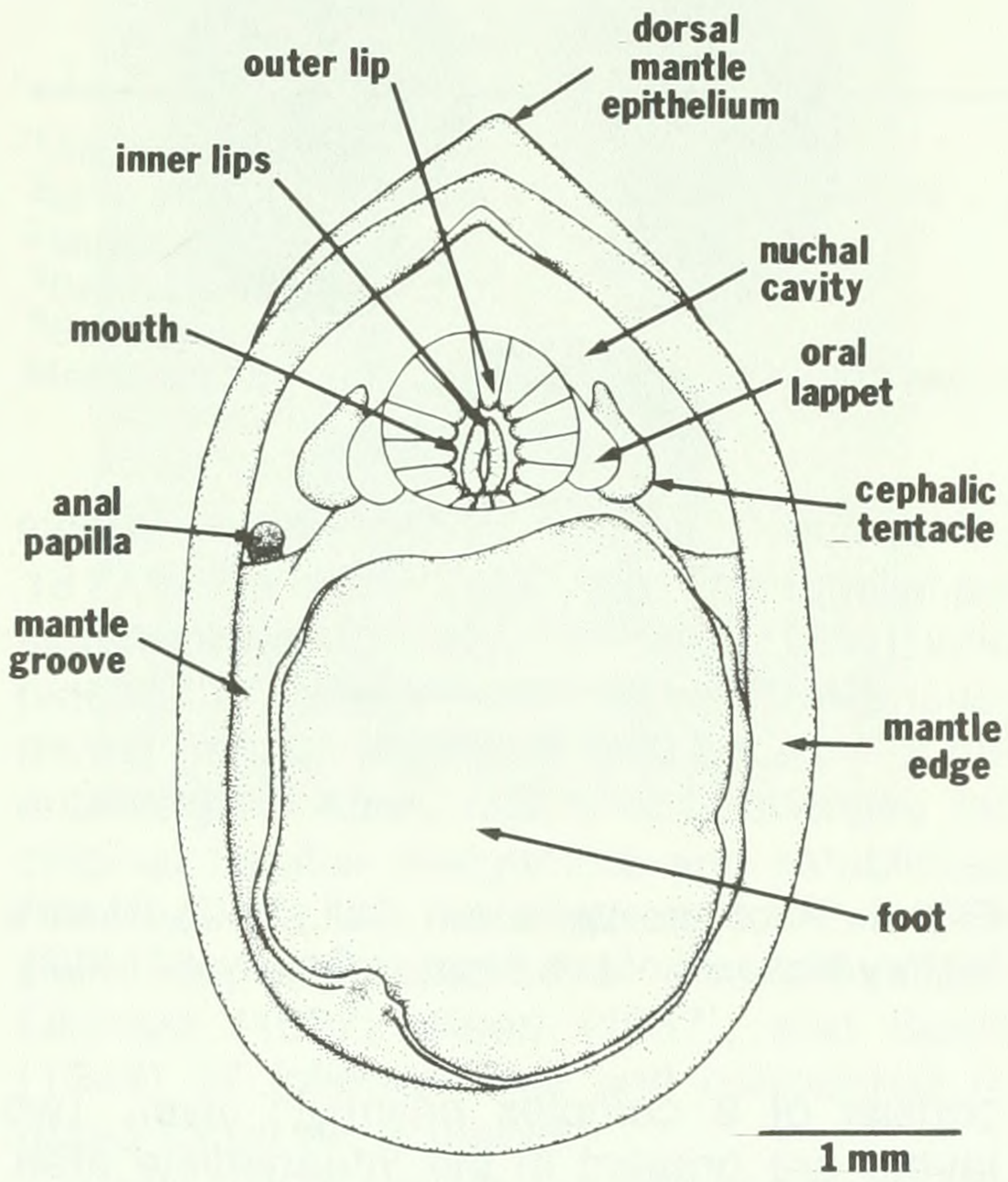

FIG. 3. Ventral view of *Rhodopetala rosea* removed from shell.

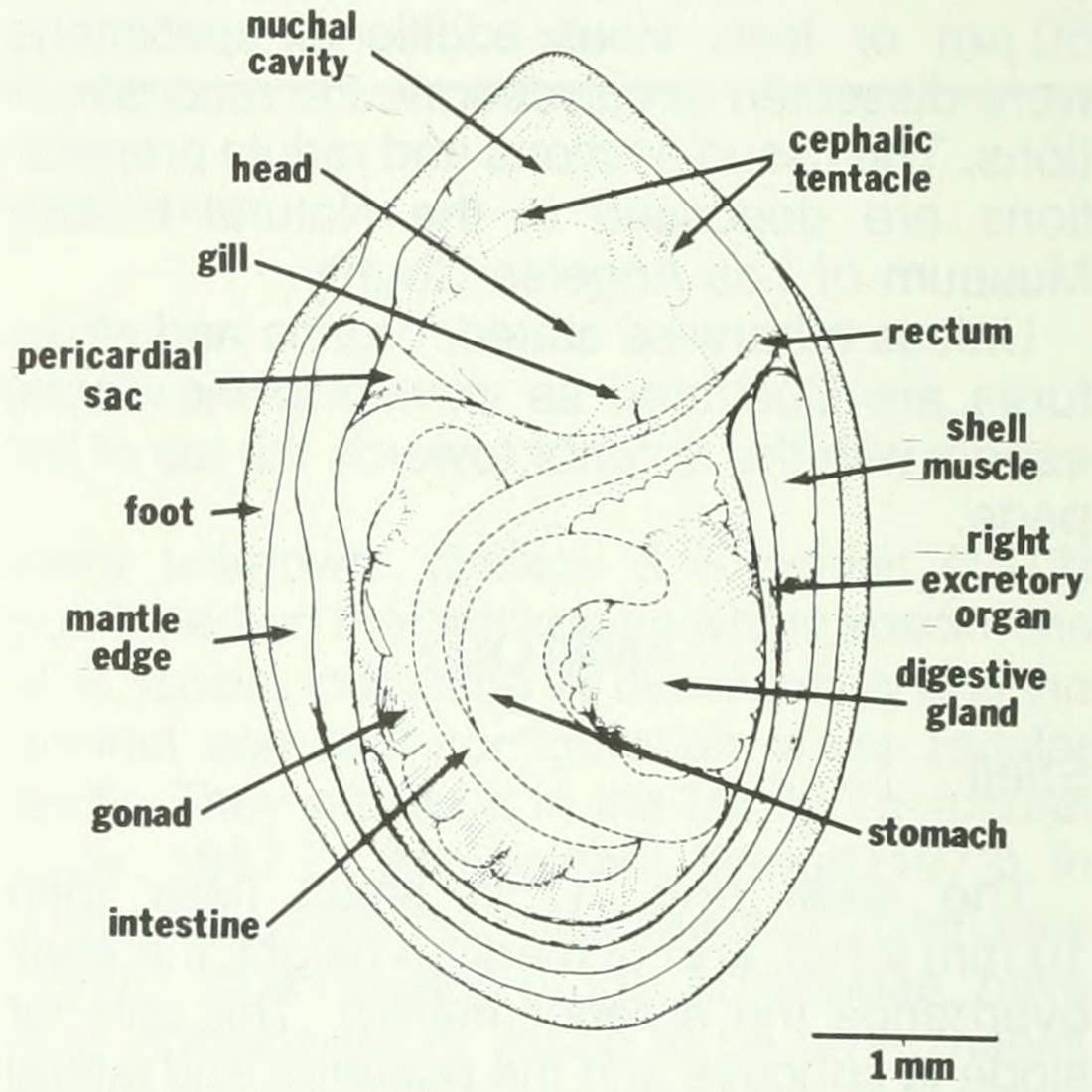

FIG. 4. Dorsal view of *Rhodopetala rosea* removed from shell.

the aperture posteriorly. The head is oval with a single pair of cephalic tentacles arising dorsolaterally. The mouth appears as a sagittal slit and is surrounded by a broad outer lip. Laterally the outer lip is drawn out into large oral lappets. The anal papilla is visible below the right cephalic tentacle. The mantle margin is thickened around the perimeter of the aperture, especially along the anterior portion of the nuchal cavity. No pallial tentacles are visible.

Viewed in the dorsal aspect (Fig. 4), the large nuchal cavity is visible at the anterior of the limpet. A small flap of tissue, the gill, is visible through the mantle in the middle of the nuchal cavity. To the left of the gill is the pericardial sac. The visceral mass is surrounded laterally and posteriorly by the shell muscle. This horseshoe-shaped muscle is made up of nondiscrete muscle bundles and opens broadly anteriorly. In the center of the visceral

mass is the kidney-shaped stomach. A lobate digestive gland is to the right of the stomach. Between the digestive gland and the shell muscle, the dorsal surface of the right excretory organ can be seen. The gonad lies to the left of the stomach and against the left shell muscle. The intestine, arising from under the posterior end of the stomach, curves around the left side of the stomach and extends diagonally across the viscera, terminating at the anal papilla, which is adjacent to the right of the gill and anterior of the shell muscle.

Internal anatomy

Nuchal cavity—The nuchal cavity is large and is 40% of the animal's total length. The anterior end of the cavity is narrowed, conforming to the submarginal apex, and the thickened mantle margin. Between the dorsal and ventral mantle epithelia is a large, continuous haemocoelic space crossed by numerous tissue strands (Fig. 5a). The ciliated posterior portion of the roof of the nuchal cavity has large concentrations of cilia on the left side. A corresponding concentration of cilia occurs on the left side of the head immediately below this region.

The single gill lies in the midline of the nuchal cavity. The gill arises from the ventral mantle epithelium, not from the posterior wall of the nuchal cavity (Fig. 6). To the right, at the base of the gill lie the left excretory organ, rectum, and right excretory organ. The anterior portions of the excretory organs extend anteriorly into the mantle skirt, and the excretory pores open ventrally. The anal papilla is elongated and directed ventrally so that it opens into the mantle groove directly in front of the shell muscle (Fig. 3). The osphradia are situated on the nape of the neck far back in the cavity. The left osphradium is larger than the right. A hypobranchial gland is not present.

Gill—The single gill (Figs. 6, 7) arises in the posterior portion of the nuchal cavity from the ventral mantle epithelium at the midline of the limpet's body. It is flat and triangular with the left side slightly longer giving the apex a hooked appearance. The gill is small, 0.62 mm wide at the base and 0.68 mm long in a specimen 7.6 mm long. The gill lacks filaments, a laterally compressed axis (septum), distinct ciliated bands, and skeletal support. It closely resembles the individual lappets that form the secondary gills found in patellid limpets and some acmaeids. Along the edge of the gill runs a marginal vessel that connects on the right side to the haemocoelic space of the roof of the nuchal cavity and on the left side to the auricle of the heart. A haemocoelic space in the central portion of the gill opens on both sides into the marginal vessel. The outer surface of the gill is folded and ciliated, with longer cilia on its ventral surface.

Digestive system—The looping of the alimentary tract is simple (Fig. 8). The esophagus lies largely to the left and rotates counterclockwise approximately 135 degrees based on the position of the dorsal folds. The posterior portion of the esophagus is slightly expanded. Directly behind the dilation it turns to the left and anteriorly broadens into a large stomach. The anterior end of the stomach turns to the right and downward. A constriction marks the begining of the intestine, which

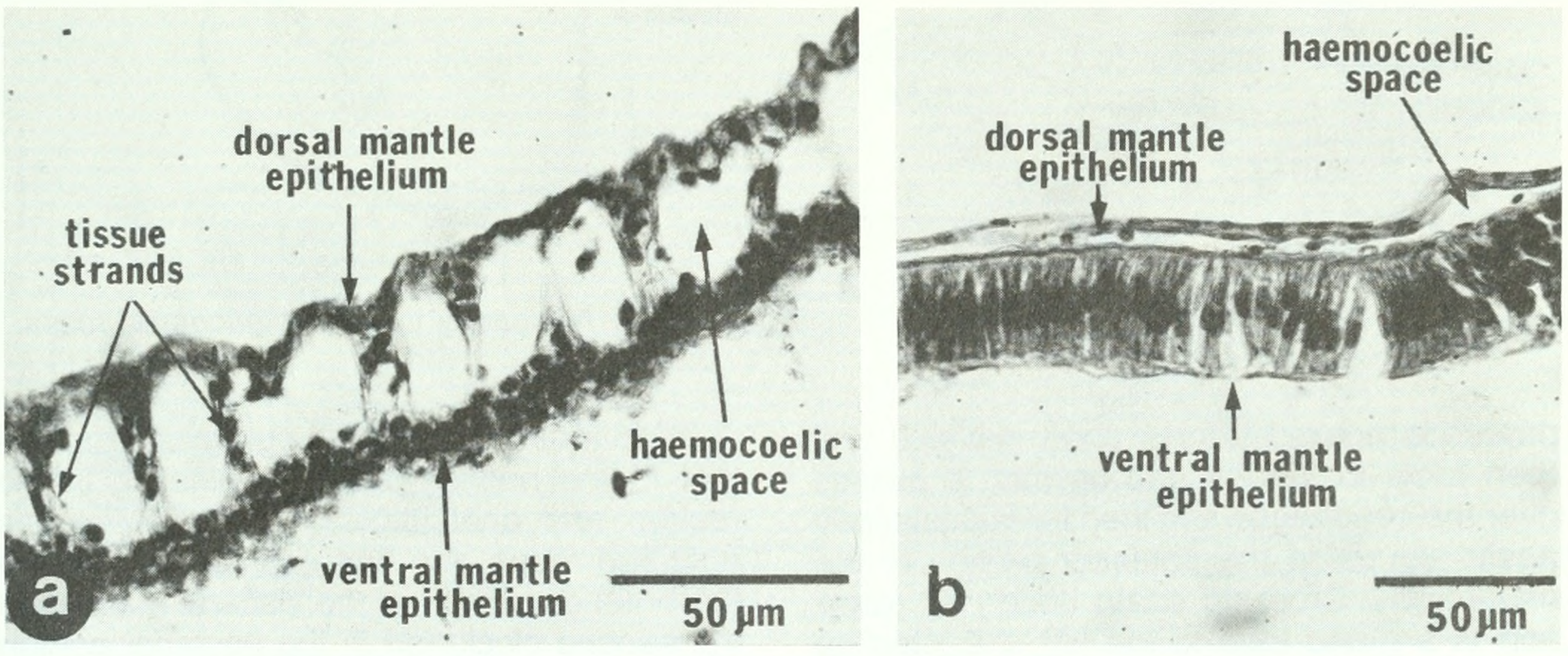

FIG. 5. Transverse section through the mantle skirt. (a) *Rhodopetala rosea,* (b) *Tectura rubella.*

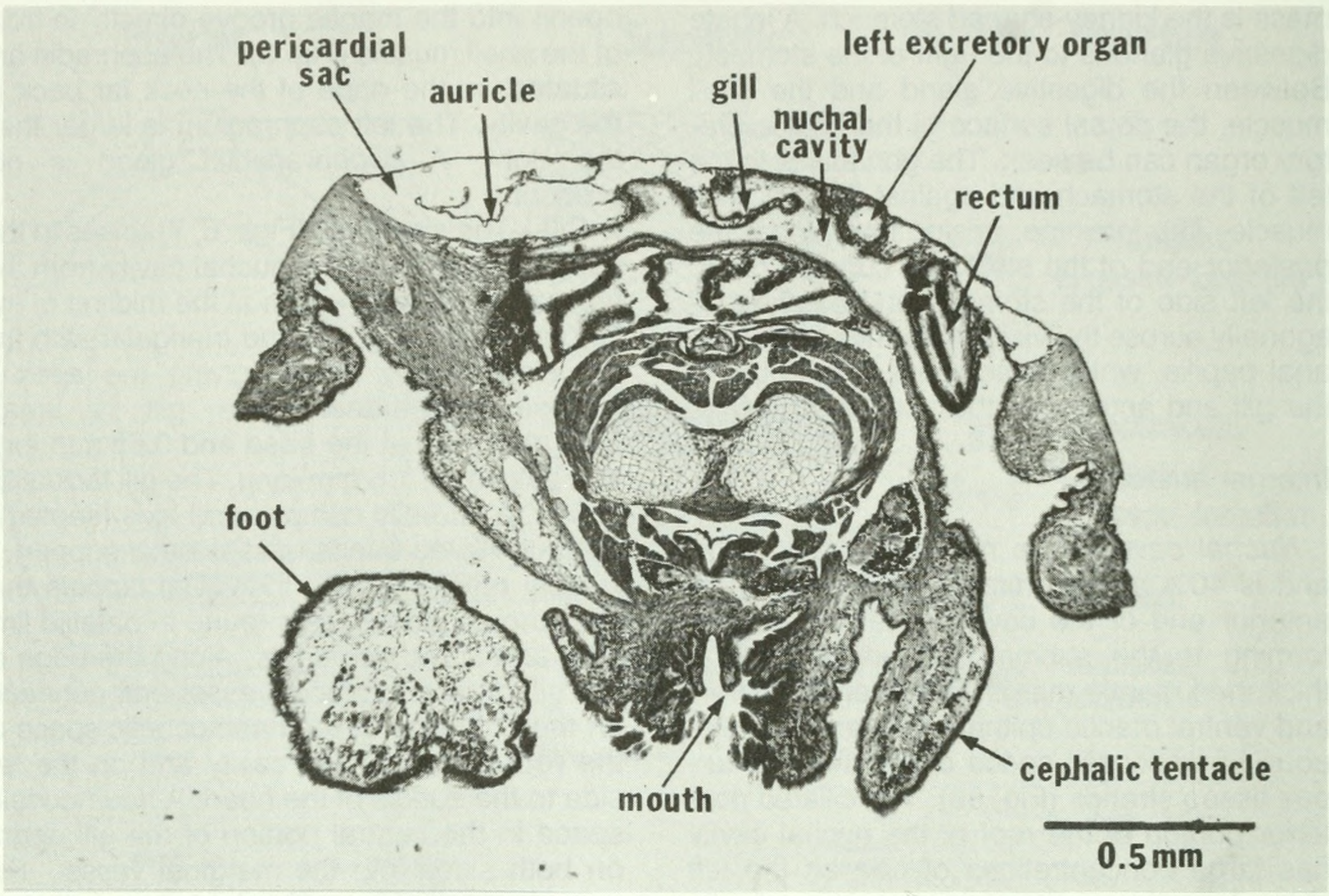

FIG. 6. Transverse section through the head and nuchal cavity of *Rhodopetala rosea.*

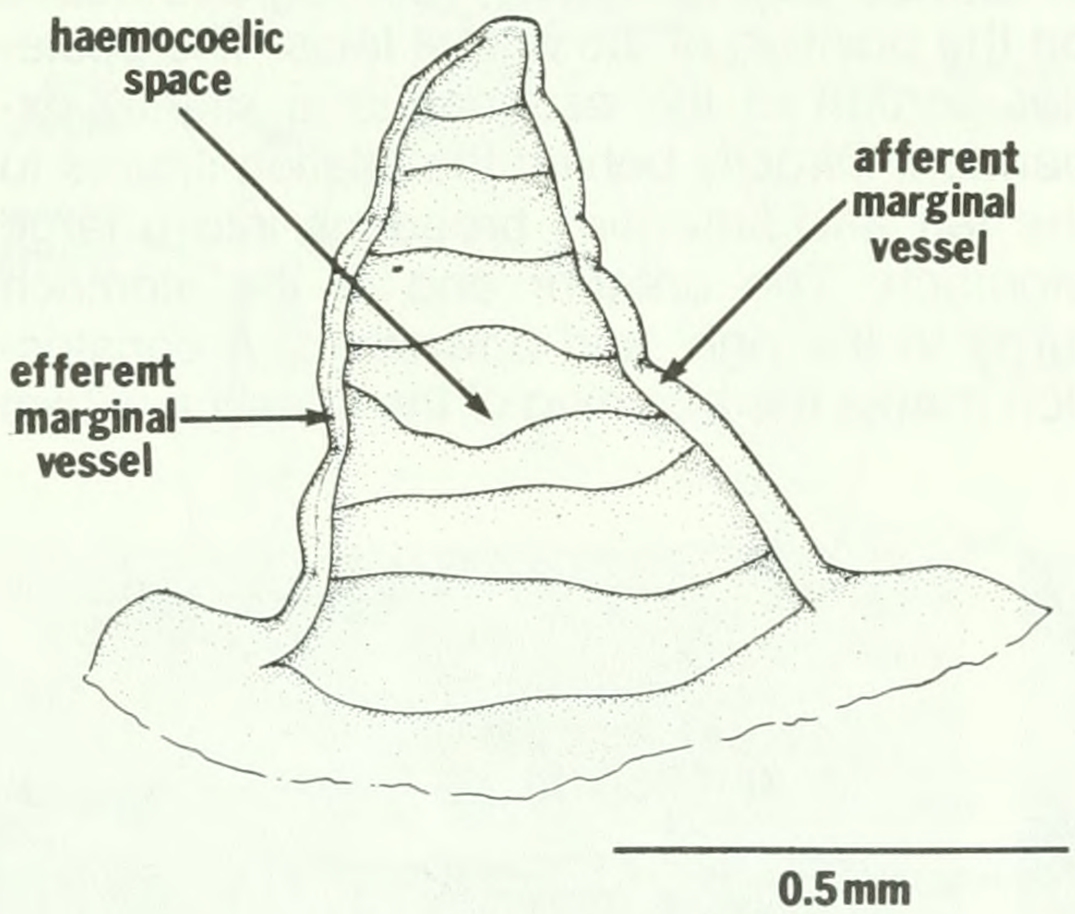

FIG.7. Gill of *Rhodopetala rosea.*

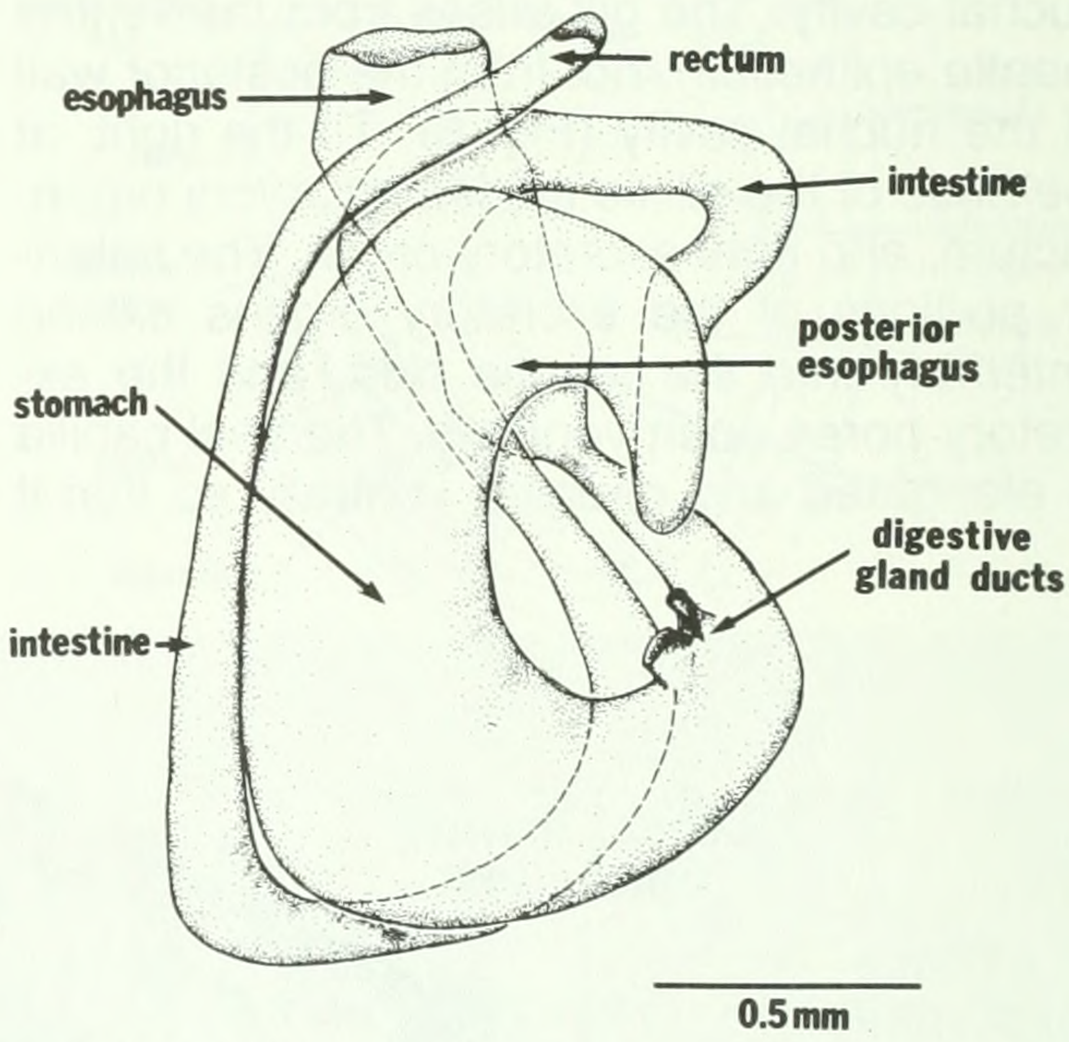

FIG. 8. Alimentary tract of *Rhodopetala rosea.*

proceeds anteriorly for a short distance and then turns to the left and upward. It passes over the esophagus and then turns posteriorly again alongside the posterior portion of the esophagus. Crossing again under the stomach in a broad loop to the left, the intestine turns anterodorsally along the left side of the stomach and finally diagonally crosses the visceral mass towards the right posterior portion of the nuchal cavity, terminating in the rectum and anal papilla. The intestine has only two loops, the first counterclockwise in the anterior portion of the visceral mass, and the second clockwise in the posterior portion of the visceral mass.

The looping of the radula is mostly in an

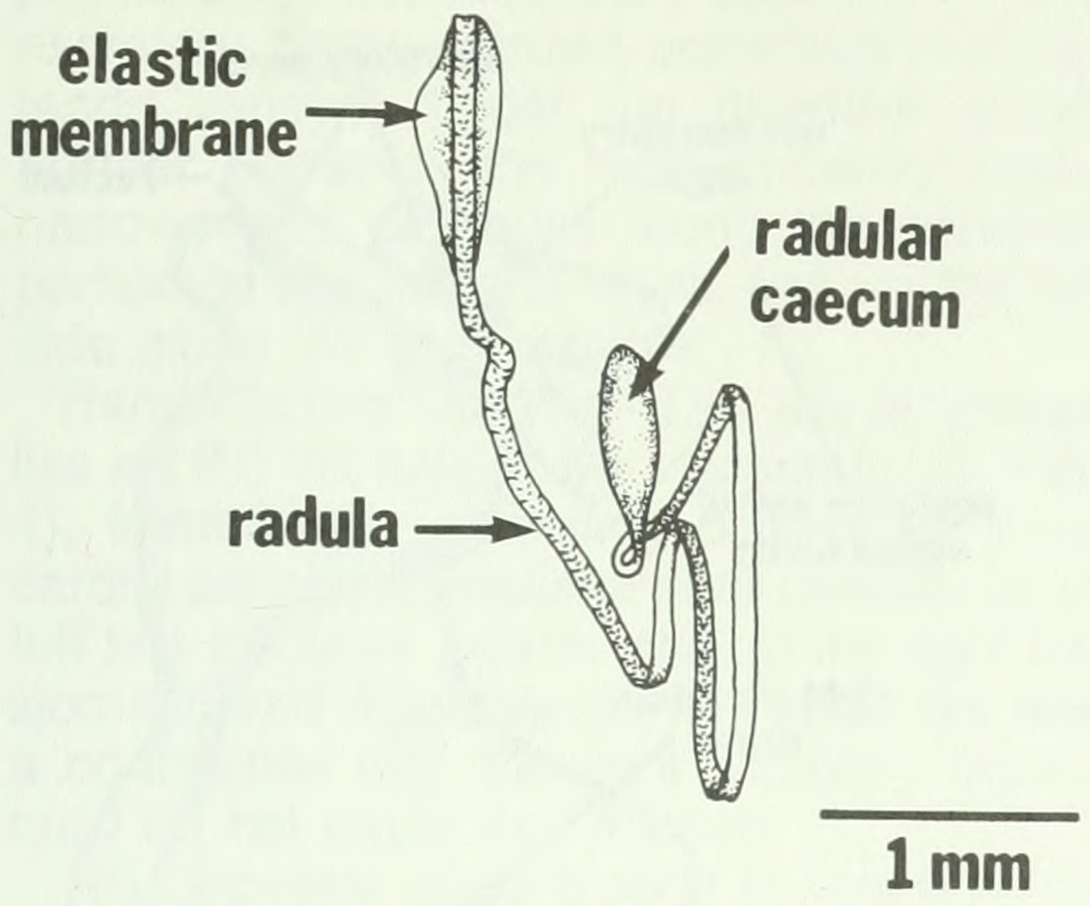

FIG. 9. Radular sac of *Rhodopetala rosea*.

oblique sagittal plane between the folds of the digestive gland (Fig. 9). Behind the head the radular sac extends diagonally along the right side of the esophagus. Immediately posterior to the cross nerve between the right and left pedal nerve cords the radula makes a U-shaped turn upward and runs anteriorly for a short distance. It then makes another U-shaped turn and proceeds posteriorly. After a third upward U-shaped turn the radula extends anteriorly again. In the vicinity of the anterior constriction of the stomach it turns downward proceeding almost to the dorsal surface of the foot where it forms a tight loop and proceeds anteriorly terminating in the radular caecum.

The radula has approximately 40 rows of mature lateral teeth and 20 rows with immature teeth. Each row bears three pairs of lateral teeth (Fig. 10a). The first pair of lateral teeth is closely set at the anterior edge of the ribbon. The medial and lateral edges of the first lateral teeth are convex. The second pair of lateral teeth are posterior and slightly lateral to the first pair; the medial edges are convex and the lateral edges concave. The third pair of lateral teeth are slightly posterior and lateral to the second pair; the medial edges are convex and the lateral edges are straight. Marginal teeth are lacking.

Radular rows consist of two ventral plates each with three lateral tooth plates (Fig. 10b). The first lateral plates are large and kidney-shaped. They extend beyond the anterior edges of the ventral plates. The second lateral plates are posterior to the first lateral plates and have straight posterior edges. The second lateral plates are separated from the third lateral plates by partial sutures. The lobate third lateral plates have lobes that extend to the margins of the ventral plates. The ventral plates are rectangular with an anterior process and posterior notch. The anterior process is rectangular and the medial edges of the processes continue under the first lateral plates forming a strong anterior suture.

The jaw of *R. rosea* (Fig. 11) is thickened medially and there are two rounded lateral extensions. The lateral edges of the extensions and the dorsal regions immediately adjacent to the medial area also are thickened.

Circulatory system—The pericardial sac lies to the left of the visceral mass against the shell muscle and behind the nuchal cavity (Figs. 4, 6). It contains a thin-walled auricle and a muscular ventricle and aortic bulb (Fig. 12). Both auricle and ventricle are attached to the right side of the pericardial sac.

Blood enters the auricle from the haemocoelic space in the roof of the nuchal cavity

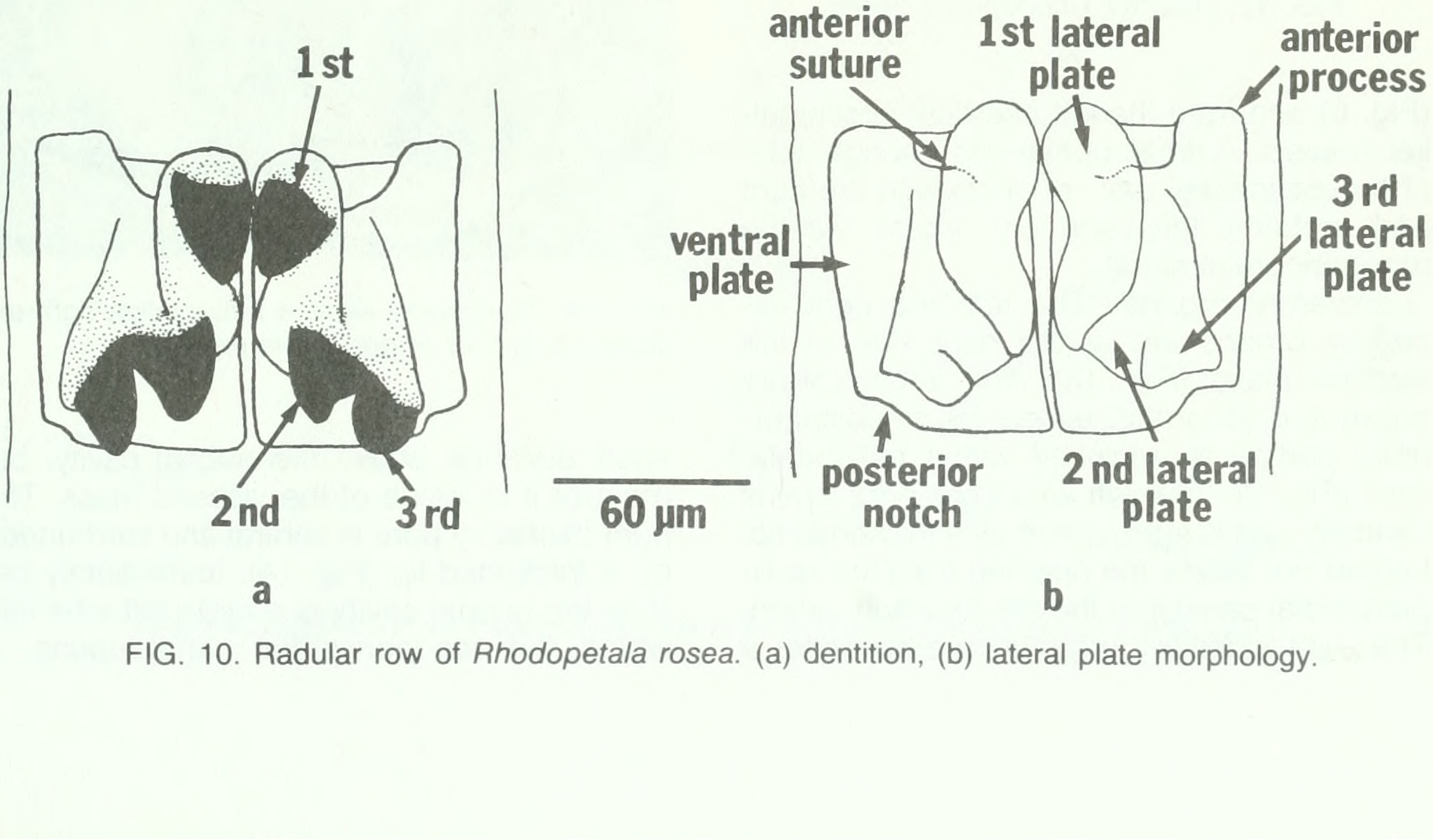

FIG. 10. Radular row of *Rhodopetala rosea*. (a) dentition, (b) lateral plate morphology.

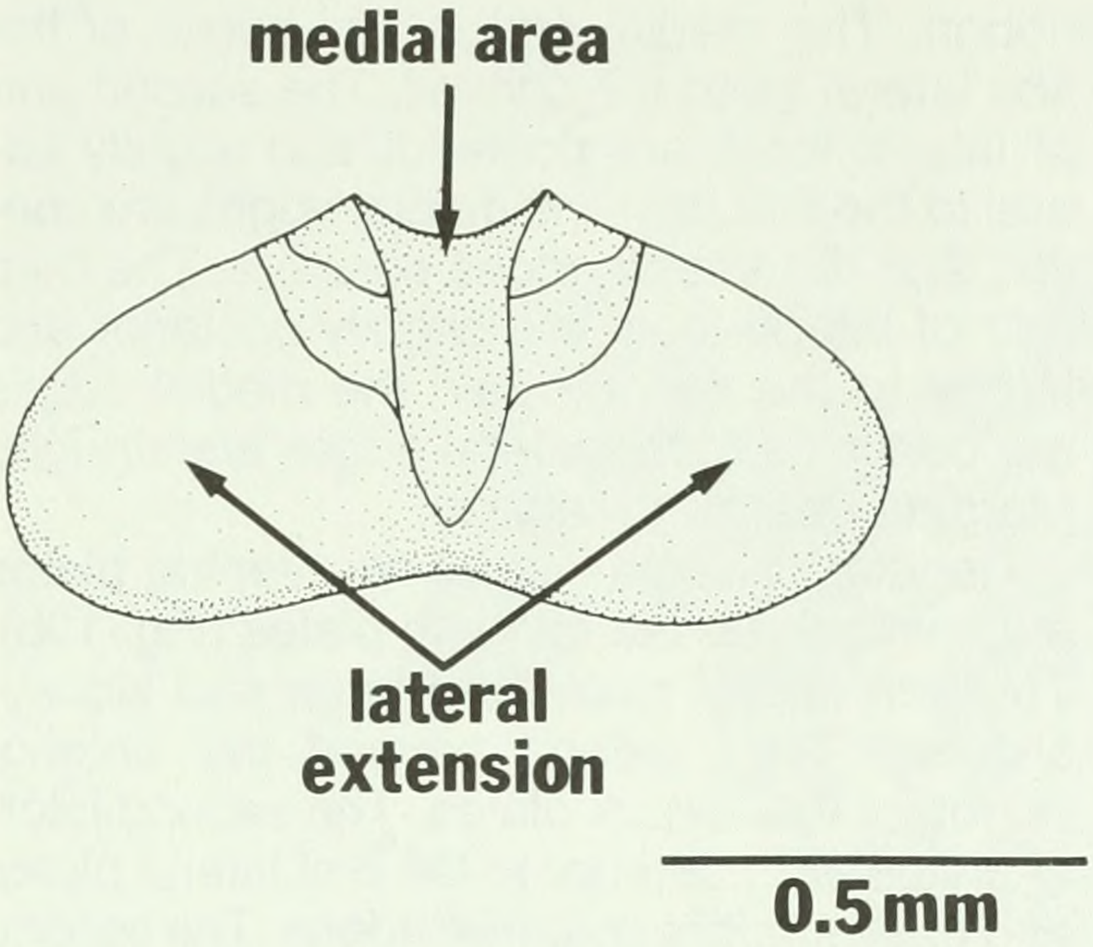

FIG. 11. Jaw of *Rhodopetala rosea.*

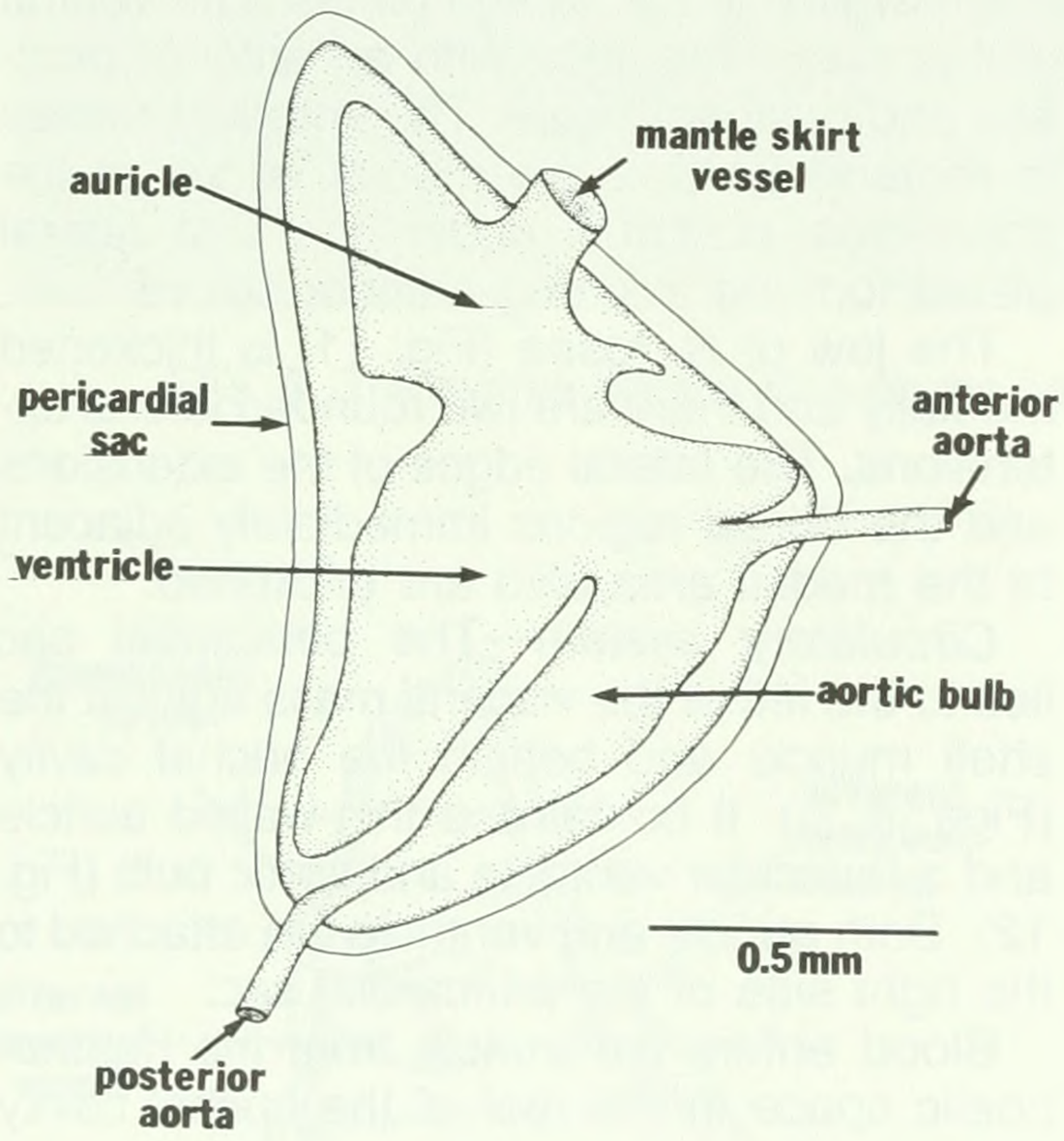

FIG. 12. Heart of *Rhodopetala rosea.*

(Fig. 6) and from the left and right circumpallial vessels. A small opening in the right lobe of the pericardial sac connects with the right and probably left excretory organs via the renopericardial canal.

Excretory organs—The left and right excretory organs are at the right side of the visceral mass (Fig. 13). The left excretory organ is oblong and, except for its posteriormost portion is enclosed within the mantle skirt (Fig. 6). The left excretory pore opens ventrally and is surrounded by a thickened lip. I could not locate the opening from the renopericardial canal into the left excretory organ. The right excretory organ also extends for a

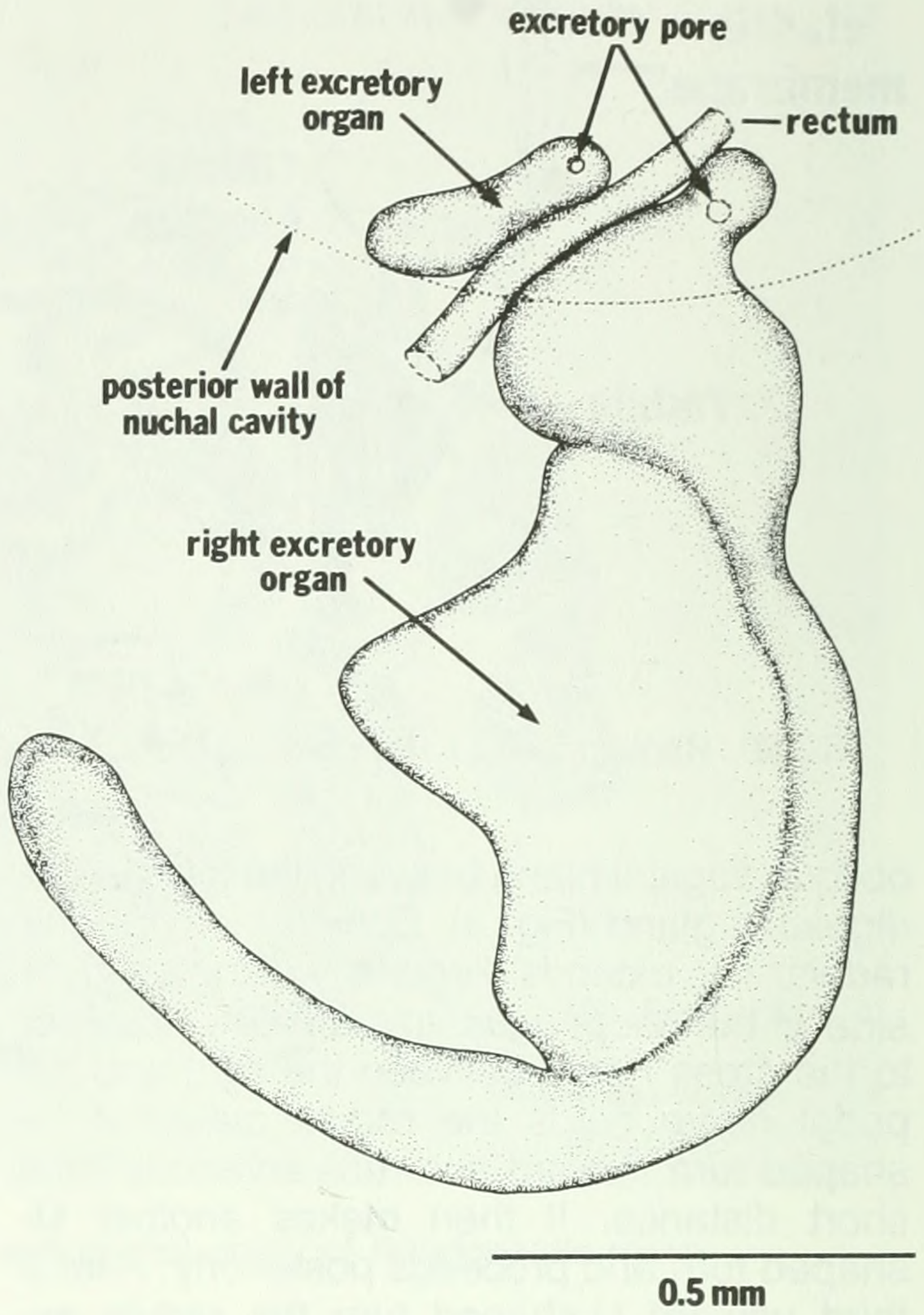

FIG. 13. Excretory organs of *Rhodopetala rosea.*

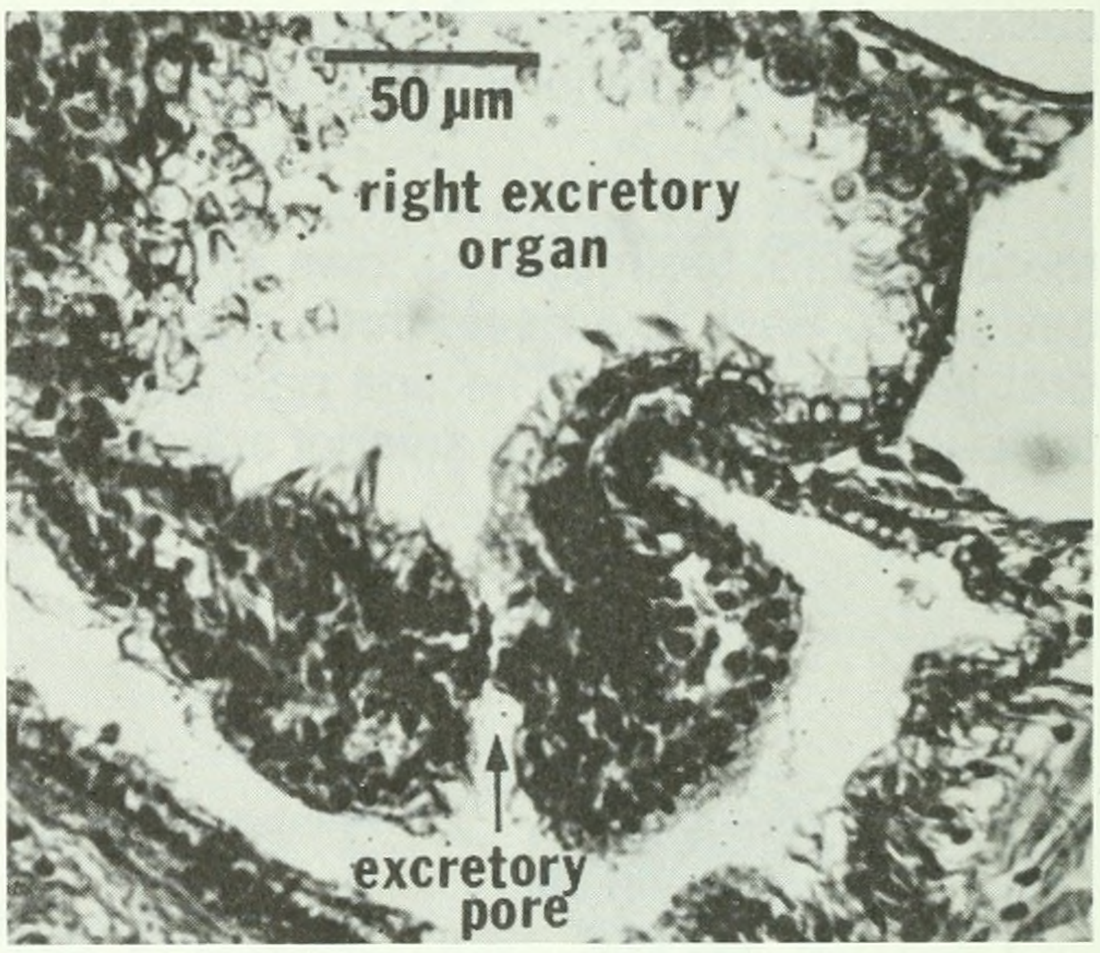

FIG. 14. Transverse section through the right excretory organ of *Rhodopetala rosea.*

short distance above the nuchal cavity, but most of it is inside of the visceral mass. The right excretory pore is ventral and surrounded by a thickened lip (Fig. 14). Immediately behind the nuchal cavity is a large left lobe into which the renopericardial canal opens; a

papilla and subanal lobe are absent. The right excretory organ narrows posteriorly and extends ventrally under the digestive gland. Further posterior, the right excretory organ narrows and continues along the posterior portion of the visceral mass and up the left side along the shell muscle.

Reproductive system—The single gonad lies on the left side of the visceral mass (Fig. 4), immediately extending behind the pericardial sac to the posterior shell muscle. To its left lies the shell muscle and on the right the stomach and digestive gland. I could not find a connection with the right excretory organ, but I do not doubt that it exists.

Rhodopetala rosea broods its young in the nuchal cavity (Golikov & Kussakin, 1972) and appears to be gonochoric unlike the hermaphroditic brooding acmaeids, *Problacmaea sybaritica* (Dall, 1871), *P. moskalevi* Golikov & Kussakin, 1972, and *Tectura rubella* (Fabricius, 1780). All 11 specimens including gravid individuals collected during the breeding season, which lasts from at least May to September, comprised separate sexes. There were no size differences suggestive of protandric hermaphroditism (Table 2).

DISTRIBUTION

USSR: Kuril Islands, Onekotan Island (49°25′N, 154°45′E) to Paramushir Island (50°25′N, 155°50′E), and ALASKA: Aleutian Islands; Rat Islands, Kiska Island (51°57′N, 178°30′E) to Afognak Island (58°21′N, 152° 30′W). Records (Fig. 15): (Western Pacific) USSR: Kuril Islands; Onekotan Island (Golikov personal communication, 1978), Paramushir Island (Golikov & Kussakin, 1972). (Eastern Pacific) ALASKA: Aleutian Islands; Rat Islands, Kiska Island (U.S. National Museum of Natural History #30789), Amchitka Island (Natural History Museum of Los Angeles County #71-252, National Museum of Natural Sciences, Ottawa #1976-30); Adak Island (San Diego Museum of Natural History #11610); Shumagin Islands, Simeonof Island [Type-locality] (U.S. National Museum of Natural History #213813, 30790, 635464): Sitkalidak Island and Afognak Island (Eyerdam, 1946).

ECOLOGY

Little is known of the ecology of *Rhodopetala rosea.* The limpets on which Golikov & Kussakin (1972) reported were collected from rocks and stones (Golikov personal communication, 1978). O'Clair (1977) reported *R. rosea* on the holdfasts and fronds of *Laminaria yezoensis* Miyabe, 1902 at Amchitka Island. Specimens were also collected from rock dominated by the coralline algae *Clathromorphum* spp. and *Thalassio-*

FIG. 15. Distribution of *Rhodopetala rosea* ● = collection records, ▲ = Attu Island.

phylum clathrus (Gmelin) Postels & Ruprecht, 1840 (O'Clair personal communication, 1979). O'Clair's specimens were collected from exposed and semiprotected intertidal areas between +2.0 feet (+0.6 m) and −2.0 feet (−0.6 m) (datum = mean lower low water). Asiatic specimens were found from the low intertidal to a depth of 10 m (Golikov personal communication, 1978).

Gut contents suggest that *R. rosea* feeds on both coralline algae and the cortical cells of laminarian algae. The shape of the radular teeth and their configuration suggests a diet of coralline algae, but bear little resemblance to those species that feed on laminarian algae (e.g. *Collisella instabilis* (Gould, 1846)). However, another species, *Collisella ochracea* (Dall, 1872), also feeds on both coralline and laminarian algae and has a radular morphology and configuration suggestive of only a coralline diet (Lindberg, 1979).

DISCUSSION

The anatomy of *Rhodopetala rosea* is basically acmaeid, with several significant differences that set it apart from other members of the family. These are seen in the shell, respiratory system, circulatory system, and in the position of the excretory organs.

The shell structure of *R. rosea* is found in 15 species of the patellid genus *Cellana* (Table 5 of MacClintock, 1967) and is characterized by a complex crossed-lamellar layer inside of the myostracum. In all other acmaeids, except *Collisella scabra* (Gould, 1846) and *C. edmitchelli* (Lipps, 1966), the layer inside the myostracum is radial crossed-lamellar. In *C. scabra* and *C. edmitchelli* the inner layer is modified foliate (Lindberg, 1978). The common shell structure of *R. rosea* and the *Cellana* species strongly suggests a phyletic relationship between the two.

The gill of *R. rosea* differs markedly in structure and orientation from those of other previously studied acmaeids. In his classic account of the pallial organs of aspidobranch gastropods, Yonge (1947: 466) described the ctenidium of the Lottiidae [= Acmaeidae] as having "the usual structure with alternating filaments identical on the two sides." The acmaeid ctenidium arises from the left posterior wall of the nuchal cavity and extends to the right across the cavity.

Yonge's (1947) description of the structure and orientation of the acmaeid ctenidium corroborates earlier studies by Willcox (1898, 1906), Fisher (1904), and Theim (1917b), and has been confirmed again in the Brazilian acmaeids by Righi (1966).

The gill of *R. rosea* arises from the nuchal cavity roof, not the left posterior wall of the nuchal cavity as reported in other acmaeids. The gill encloses a haemocoelic space through which the blood flows between marginal vessels (Fig. 7). Ctenidial filaments and distinct bands of cilia are absent. The only ciliary concentration is a group of long cilia on the left ventral surface. Similar outpocketings of the ventral mantle epithelium in the nuchal cavity of the lepetid limpet *Iothia coppingeri* Smith, 1882 have been reported by Moskalev (1977).

The gill of *R. rosea* appears analogous to the individual lappets that form the secondary gill of patellid and some acmaeid limpets. Each lappet has a marginal vessel that connects with a central haemocoelic space (Gibson, 1887; Davis & Fleure, 1903; Nuwayhid & Davies, 1978).

Structures of the digestive system of *R. rosea* are acmaeid-like. Whereas the patellid intestine typically has numerous, complex loops (Davis & Fleure, 1903; Fleure, 1904; Graham, 1932; Graham & Fretter, 1947), *R. rosea* has a simply looped intestine similar to eastern Pacific acmaeids (Walker, 1968). The esophagus of *R. rosea* is rotated approximately 135 degrees. Fleure (1904) reported that the maximum rotation of the acmaeid esophagus is 250 degrees, while in the Patellidae it is 270 to 330 degrees. While I cannot account for the limited rotation in *R. rosea,* it is far below the 270 degree minimum given for the Patellidae. The radula loops between the lobes of the digestive gland in a pattern similar to that of other eastern Pacific acmaeids (Walker, 1968), and not like that of *Cellana* species with which *R. rosea* shares shell structure (Theim, 1917a). The radular dentition and basal plate morphology are distinctly acmaeid. Although the radular teeth bear a superficial resemblance to those of *Acmaea* s.s. Eschscholtz, 1833, the complexity of the basal plates more closely resembles those found in members of the genera *Collisella* Dall, 1871 and *Notoacmea* Iredale, 1915.

The heart of *R. rosea* has both acmaeid and patellid features. In other acmaeids the efferent blood vessel from the ctenidium connects directly to the auricle (Willcox, 1898, 1906; Fisher, 1904; Fleure, 1904; Theim, 1917b; Righi, 1966; Kingston, 1968), and the

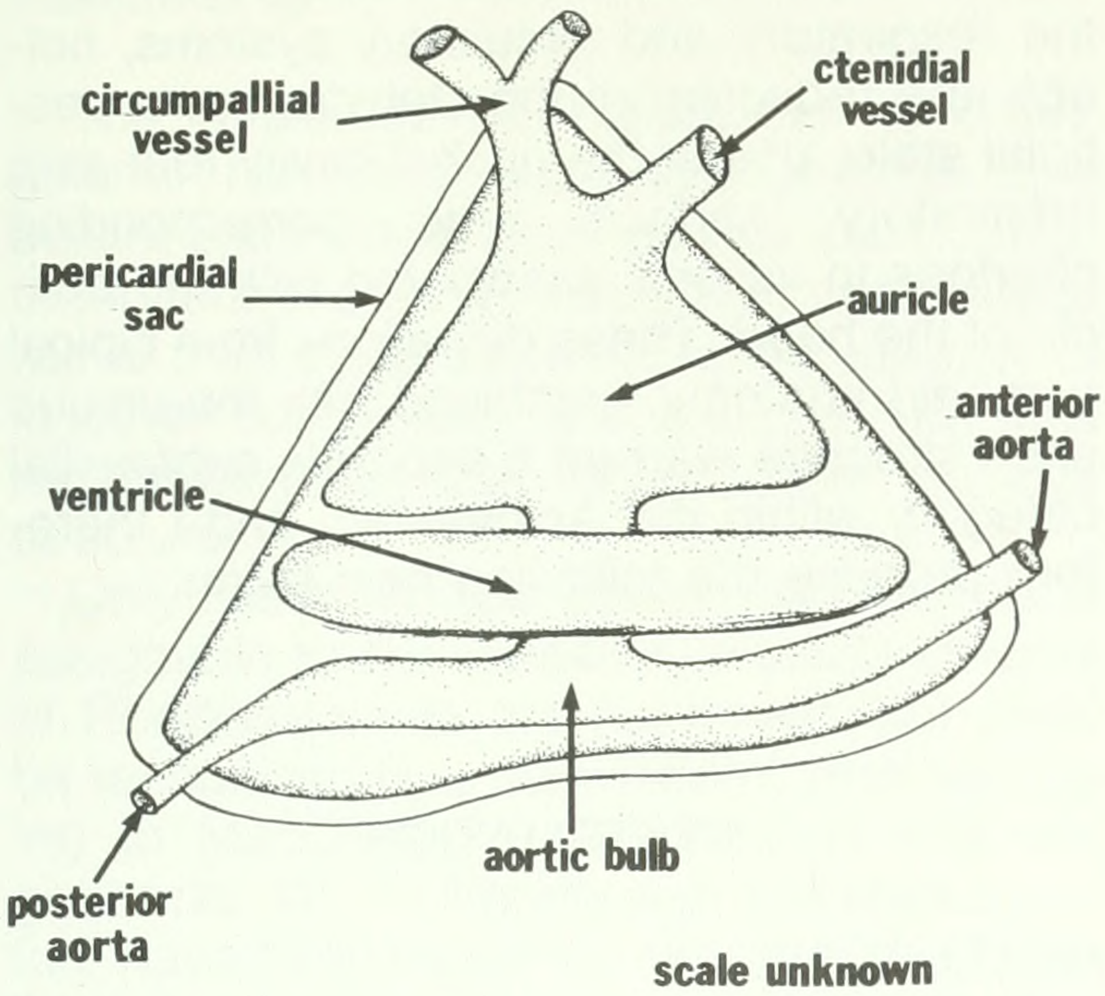

FIG. 16. Heart of acmaeid limpet. Redrawn from Fleure (1904).

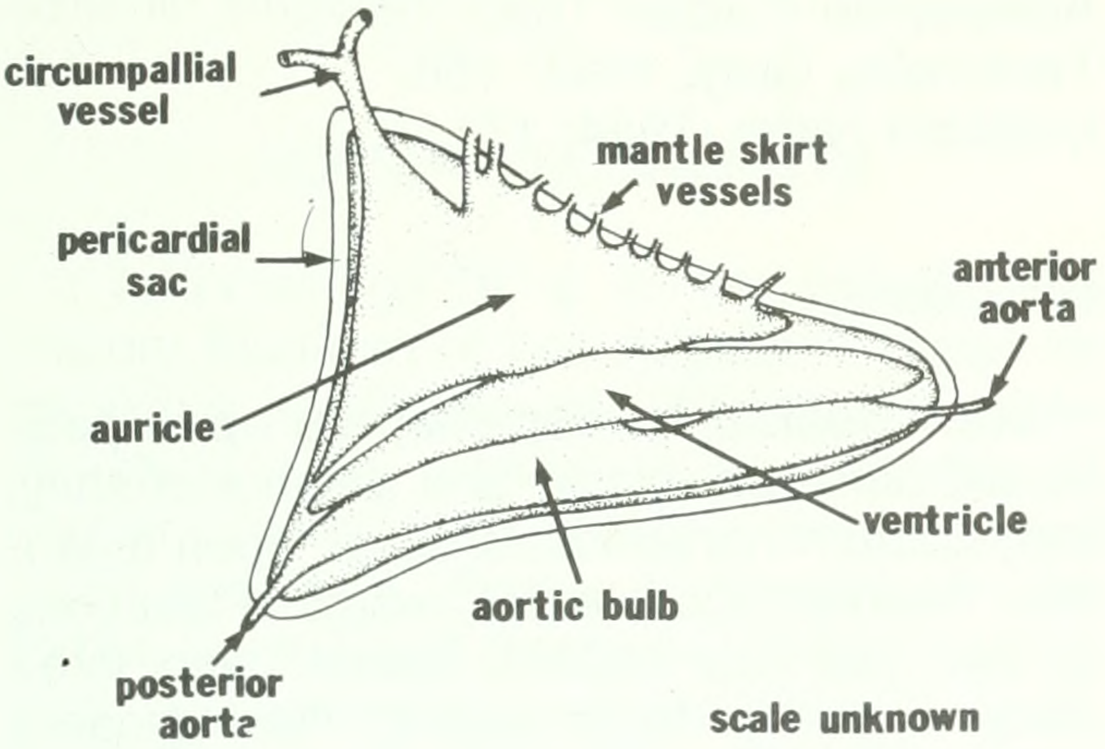

FIG. 17. Heart of patellid limpet. Redrawn from Fleure (1904).

circumpallial vessel enters the auricle immediately to the left of the ctenidial vessel (Fig. 16). The patellid heart (Fig. 17) is identical to the acmaeid heart but patellids lack a ctenidium and there is no ctenidial vessel. Instead, blood enters the auricle from the porous roof of the nuchal cavity (Fleure, 1904). As in acmaeids, blood also enters the auricle from the circumpallial vessel. *Rhodopetala rosea,* like other acmaeids, has a connection between the gill and auricle, but it is not a distinct vessel. Instead, blood from the gill is collected in the haemocoelic spaces that communicate with other haemocoelic spaces of the nuchal cavity roof. Here, blood passed through the gill is mixed with blood passed only through the nuchal cavity roof before it enters the auricle. There is not a distinct connection between the auricle and the circumpallial vessel. Instead, blood from the circumpallial vessels enters the porous roof of the nuchal cavity and proceeds to the heart. In this respect vessels of the auricle differ from both patellids and acmaeids (cf. Figs. 12, 16, 17).

The small size and rudimentary state of the gill of *R. rosea,* combined with the modifications of the auricle, suggest that the nuchal cavity roof is an important site for respiration. This same surface is thought to be a respiratory surface in the Patellidae (Fleure, 1904) and in other prosobranchs (Hyman, 1967: 205).

Typically in the Acmaeidae, the inner surface of the mantle margin is a secondary surface for respiration (Fisher, 1904; Kingston, 1968). Located here is the circumpallial sinus from which highly branched vessels arise and anastomose. Blood passes through this sinus before it is recollected and returned to the auricle through the circumpallial vessels. The tiny circumpallial sinus of *R. rosea* does not appear to be developed for respiration. Gas exchange on the mantle margin would be insignificant to gas exchange in the nuchal cavity roof through which all blood returning to the auricle passes. It is not clear if the roof of the nuchal cavity is a respiratory surface in other acmaeids. Circulatory patterns, as demonstrated with injection of dye in live and preserved specimens, have not implicated the roof of the nuchal cavity for respiration in other eastern Pacific species (Fisher, 1904; Kingston, 1968). Moreover, there are structural differences in the nuchal cavity roof of different species. Righi (1966: fig. 8) illustrated a large haemocoelic space in the roof of the nuchal cavity of *Collisella subrugosa* (Orbigny, 1841). In contrast, *Tectura rubella,* a brooding circumarctic species, has a very weakly developed space (Fig. 5b).

The excretory organs of other acmaeids and patellids lie behind the posterior wall of the nuchal cavity, the left excretory organ is much smaller than the right, and both open into the nuchal cavity through anterior excretory pores (Lankester, 1867; Gibson, 1887; Willcox, 1898, 1906; Davis & Fleure, 1903; Fisher, 1904; Theim, 1917b; Righi, 1966; Walker, 1968). In *R. rosea* the excretory organs are not totally behind the posterior wall of the nuchal cavity. Except for the posteriormost portion, the left excretory organ is within the mantle skirt above the nuchal cavity (Fig. 6). A corresponding portion of the larger right excretory organ also extends over the nuchal

cavity within the mantle skirt, but the bulk remains in the visceral mass. In addition, the excretory pores open ventrally into the cavity, not anteriorly as in other species. Otherwise, the location and size of the excretory organs are as in other acmaeids; the subanal lobe of the right excretory organ, reported in the Patellidae by Lankester (1867) is not present in *R. rosea.*

The reproductive systems of patellid and acmaeid limpets are very similar. In both families the gonad originates as a flat tubular structure appressed to the dorsal surface of the foot on the left side of the visceral mass. When gravid, the acmaeid gonad lies ventral to the visceral mass (Fisher, 1904; Righi, 1966; Walker, 1968). In the patellids, the gravid gonad lies ventral to the visceral mass, but also extends up the left side along the shell muscle (Gibson, 1887; Davis & Fleure, 1903; Branch, 1974). The presence of the gonad of *R. rosea* on the left side of the visceral mass appears to be a patellid feature.

The haemocoelic space in the nuchal cavity roof, the modifications of the circulatory system, and the position of the anterior portions of the excretory organs may be modifications of the nuchal cavity associated with brooding. The presence of young in the nuchal cavity would undoubtedly hamper water circulation and gas exchange along a typical ctenidium; thus modifications of the nuchal cavjty roof for gas exchange may be an adaptation to increase the respiratory surface area. Correspondingly, circulatory patterns would be modified to ensure that oxygenated blood from the nuchal cavity roof would flow directly to the heart. Because of the rich blood supply of the excretory organs, the placement of the anterior portions in the mantle skirt may also serve to increase the respiratory surface (Fretter, personal communication, 1979).

Initially I thought that the disjunct distribution of *R. rosea* was an artifact of incomplete collecting in the Aleutian Islands. However, thorough searches of intertidal and subtidal localities on Attu Island (Fig. 15) over a 5 week period failed to procure a single specimen of *R. rosea.* Therefore, the disjunct distribution of *R. rosea* may, in part, be real.

In summary, the anatomy of *R. rosea* indicates that this species is an acmaeid limpet. The distinguishing characters are a gill in the nuchal cavity, rotation of the esophagus, looping of the intestine and radula, radular dentition, and the proportions of the right excretory organ. Major modifications have occurred in the respiratory and circulatory systems, notably the reduction of the ctenidium to a vestigial state, use of the nuchal cavity roof as a respiratory surface, and corresponding changes in vessels associated with the auricle of the heart. These deviations from typical acmaeid anatomy, combined with the unique shell structure warrant a separate subfamilial category within the Acmaeidae, and I therefore propose the following new taxon.

SYSTEMATICS

MOLLUSCA
Gastropoda Cuvier, 1797
Archaeogastropoda Thiele, 1925
Patellacea Rafinesque, 1815
Family Acmaeidae Forbes, 1850
Acmaeidae Forbes, 1850: 76.
Tecturidae Gray, 1847: 158.
Lottiidae Habe, 1944: 171.

Diagnosis

Shell conical or cap-shaped, apex positioned between middle and anterior of shell; myostracum horseshoe-shaped, open anteriorly. Radula docoglossate; marginal teeth one or two pairs or absent, lateral teeth three pairs, rachidian tooth lacking. Nuchal cavity with single gill; secondary gill in mantle groove present in some genera.

Triassic to Recent.

Rhodopetalinae subfam. nov.

Type-genus *Rhodopetala* Dall, 1921: 171.

Diagnosis

Shell helcioniform, apex positioned at anterior quarter of shell, submarginal. Marginal teeth lacking, lateral teeth approximately equal in size and shape. Gill rudimentary, situated medially at back of nuchal cavity; secondary gill absent. Shell structure of 5 layers, outer surface and interior margin complex prismatic, followed by foliate, radial crossed-lamallar, myostracum, and complex crossed-lamellar layers.

Recent.

Remarks

The subfamily Rhodopetalinae is distinguished from other acmaeid subfamilies by a helcioniform rather than conical shell, an interior central area with a silvery metallic lustre rather than a porcelaneous central area found in other subfamilies, and the presence of a rudimentary gill that lacks typical ctenidial structures.

Only the monotypic genus *Rhodopetala* is assignable to this subfamily. Fossil members of Rhodopetalinae are not known, but could be recognized by a helcioniform shell belonging to MacClintock's (1967) shell structure group no. 12. All limpets with this shell structure have been thought to belong to the Patellidae, but I believe that the group no. 12 shell structure and the acmaeid-like anatomy suggest that the Rhodopetalinae is an ancestral intermediate group between acmaeid and cellanid limpets.

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